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Genetic and hormonal control of vascular tissue proliferation

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The plant vascular system develops from a handful of provascular initial cells in the early embryo into a whole range of different cell types in the mature plant. In order to account for such proliferation and to generate this kind of diversity, vascular tissue development relies on a large number of highly oriented cell divisions. Different hormonal and genetic pathways have been implicated in this process and several of these have been recently interconnected. Nevertheless, how such networks control the actual division plane orientation and how they interact with the generic cell cycle machinery to coordinate these divisions remains a major unanswered question.

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Introduction

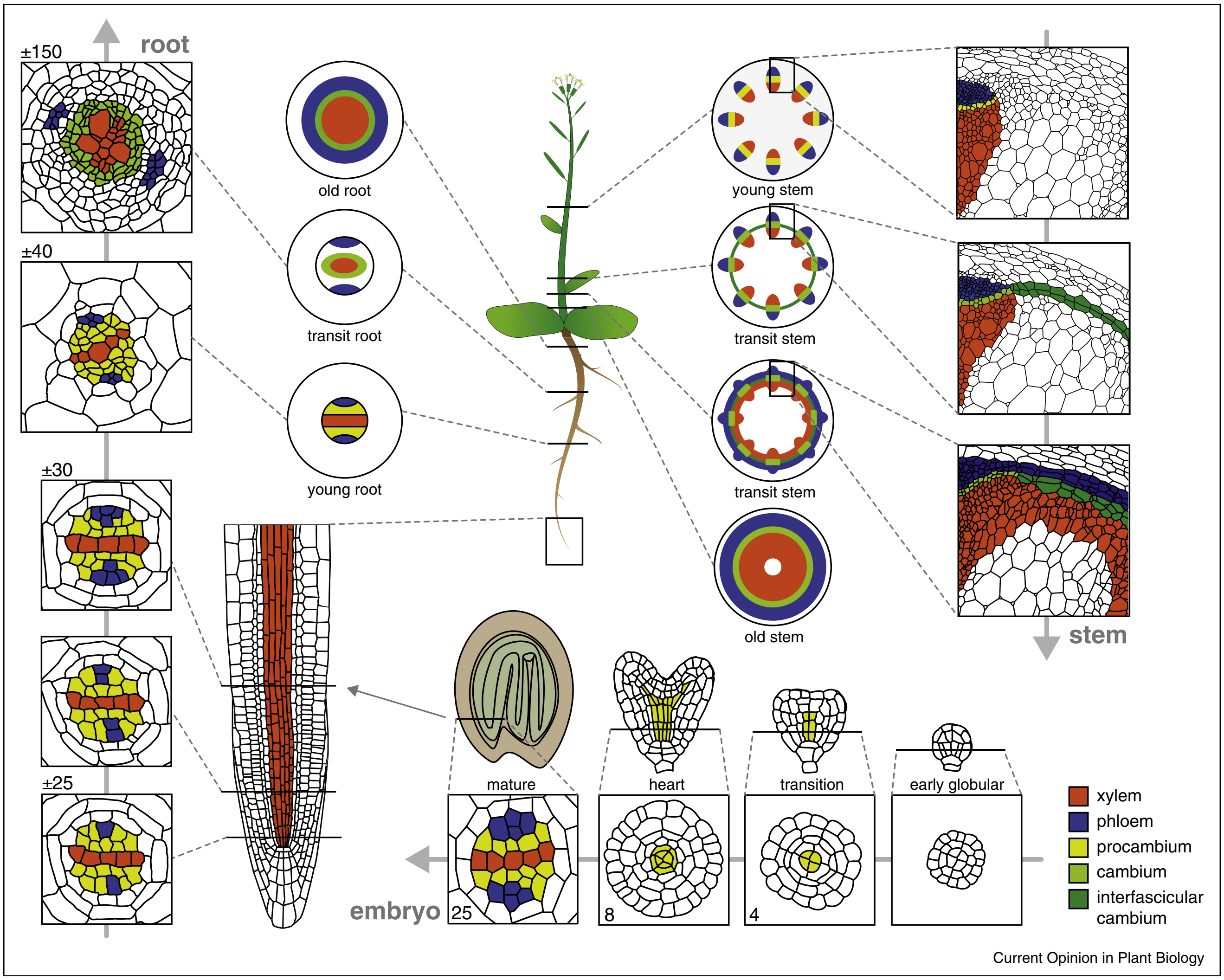
Vascular tissues form an efficient fluid conducting system that stretches throughout the entire plant body. Besides providing long-distance transport of water, sugars, nutrients, hormones and other signaling molecules, it also contributes to mechanical support. Broadly speaking, the vascular system consists of three major tissue types: xylem, phloem and (pro)cambium cells (Figure 1). On the basis of ontogeny and anatomical studies during embryogenesis and in the primary root meristem, it seems that all vascular cell types are derived from procambium cell divisions [1,2,3••,4]. Although the organization of vascular tissues differs tremendously between species, within different organs and even depending on the developmental stage, procambium is in general located between xylem and phloem cell types (Figure 1). Xylem tissues differentiate into several cell types including tracheary elements, xylem fibers and xylem parenchyma cells. Each of these xylem cell types contain distinct lignified secondary walls that combine the required mechanical strength with connectivity between cells [5,6]. Phloem on the other hand, consists of sieve elements, companion cells, phloem fibers and phloem parenchyma cells. Intriguingly, the different vascular cell types described above all originate from only a few procambium initial cells in the early embryo. Unlike for example epidermis and cortex, procambium cells thus need to develop into a vast array of cell identities; a process that is dependent on specific oriented cell divisions.

In the following, we will illustrate how these oriented cell divisions are critically involved in developing an efficient vascular system and we will highlight how genetic and hormonal regulatory networks control vascular proliferation. Because most of these interaction networks have been best described in *Arabidopsis thaliana*, we will focus on this model species. For a more comprehensive overview of the different vascular cell types and their function, we refer to some excellent recent reviews [7–11].

Oriented cell divisions shape the vascular cell lineage

Because plant cells have rigid cell walls and are immobilized within a tissue context, cell expansion and oriented cell divisions are the main mechanisms to shape a three-dimensional organ and eventually the entire plant body. Two basic types of divisions occur in plants: perpendicular (anticlinal) and parallel (periclinal) to the surface of the plant (Figure 1). An anticlinal cell division (AD) adds a new cell to an existing cell file and is thus the main driver of longitudinal growth along the main body axis of the plant. A periclinal cell division (PD) however provides an increase in the number of cell-files and thus control radial growth. These divisions often result in daughter cells of different size or identity and are therefore also referred to as 'formative divisions' [12]. The existence of these clearly distinct division types also suggests that control mechanisms must be present to specifically position the division plane and control its orientation. This process plays vital roles throughout plant development, starting with the very first division of the zygote [13,14]. Later during embryogenesis, specific anticlinal and periclinal cell divisions generate all major tissue types of the plant [1,2]. Post-embryonically, cell division orientations have also been shown to be of vital importance in for example root stem cells [15],

Figure 1



An overview of how periclinal cell divisions contribute to shaping the vascular cell lineage throughout plant development. Starting from only four procambium cells in the early embryo (bottom panel) periclinal divisions increase the number of vascular cell files both in root (left panel) and in stems (right panel). The vascular tissues of the shoot and root lateral organs are omitted for simplicity. The location of each cross section is indicated on a young *Arabidopsis thaliana* plant in the middle. The representative location of the section through the mature embryo in comparison to the post-embryonic root meristem is indicated with a thin arrow. The large gray arrows behind the cross sections represent the time axis during development and the numbers on or next to the cross sections represents the number of cells within the vasculature (excluding the pericycle cells). Note that two of the four procambium cells in the early globular stage embryo share a common cell wall, predicting the future xylem axis.

stomatal development [16] and lateral root formation [17,18].

Although a tight control of cell division orientation is important throughout plant development, this is specifically true for vascular tissues. During the early globular stage of embryogenesis, four procambium cells expressing early vascular marker genes [19] will undergo a series of PDs giving rise to a fully patterned vascular bundle containing about 25 cell files (excluding pericycle cells) in a mature embryonic root (Figure 1). In *Arabidopsis*, the young root vasculature is organized in a bisymmetric pattern with a central one-cell wide xylem axis, flanked by two phloem poles and separated by procambium. Additional rounds of post-embryonic PDs in the meristematic vascular tissues will further increase the number of vascular cell files from 25 just above the quiescent center to about 30 in the elongation zone (Figure 1). Of particular interest in this case is the phloem cell lineage. Here, a single procambium cell undergoes a PD resulting in another procambium cell and a sieve element precursor cell. The latter undergoes another round of PD, generating a proto-phloem and a meta-phloem cell file (Figure 1). Two more PD events generate the companion cell files on